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EUPLOTES WORCESTERI SP. NOV.: II.1 DIVISION.

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The literature on division in the family of the Euplotide is surprisingly limited, considering its wide distribution, the ease with which observations can be made upon several of the species, the interesting processes involved, and the number of competent naturalists who have made observations on the group. The only important paper dealing with this subject is the excellent article of Wallengren upon the processes of construction and resorption occurring during division in the Hypotricha; Euplotes harpa is the principal type of this study. Wallengren then critically compares the accounts of Stein, Möbius, Maupa, and Schuberg concerning Euplotes charon, E. patella, and E. harpa. All of the accounts are very incomplete and, like that of Wallengren himself, are confined to the external changes. Wallengren has made a very careful study of the formation of the new peristome and of the origin of the new cirri during the division of Euplotes harpa, and of the resorption of the old set of cirri which are replaced by the new ones formed. Further reference will be made to this article as my description of the processes occurring in Euplotes worcesteri progresses. Unfortunately, I was not able to secure the original article of Wallengren until after my paper was ready for the press; my observations upon the origin of the peristome were therefore entirely independent. Since reading Wallen-

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gren's paper I have added nothing to my own except the necessary critical comparisons; the observations stand as originally made.

It is evident that processes of divison must be much alike in all the species of the genus Euplotes, though such differences exist as to render a comparative study extremely interesting. In considering the process of division I have omitted all reference to the divisions of conjugation and to the construction and resorption of organs during that phase, because my study of conjugation in Euplotes worcesteri, so far very incomplete, has convinced me that these processes are quite different from the ones of ordinary division. It has proved easy to keep the strain alive in the laboratory for more than a year and a half, and to secure an abundance of material for study and preparation in every possible manner. The result has been not only to prove that the new peristome is actually formed by an invagination, but also to reveal other curious processes connected with division. After an intimate study of a protozoan like this, one can appreciate the full force and meaning of the statement that many of the protozoa are not simple, but extremely complex animals.

The process of division of Euplotes worcesteri includes two stages, one of preparation, the other that of actual division of the body and meganucleus. During each stage a definite series of changes occurs in nearly every organ of the body. The stage of preparation for division includes the reconstruction and concentration of the meganucleus, the invagination of the rudiment of the new peristome, the division of the micronucleus, and the appearance of the new cirri. That of division includes the constriction of the body and separation of its halves, the drawing of the new peristome to the surface of the body and into its final shape and position, completion of the new pharynx, division of the meganucleus, absorption of the old cirri, and the shifting of the new cirri from the places of their origins to their ultimate positions.

RECONSTRUCTION OF THE MEGANUCLEUS.

By this is meant that a progressive change occurs in which all the chromatin of the meganucleus is actually dissolved and then reconstructed. The first stage of this process is the appearance at each end of the cord-shaped meganucleus of a band in which there is a complete absence of the ordinary chromatin reticulum. It will be convenient to refer to these as the reconstruction bands. They pass rapidly from the ends of the nucleus toward the center, finally meeting, and then disappearing. (Plates IV, V, and VI, figures 1, 2, 3, 4, 8, 10, 13, 14, 18, 20.) Each band consists of two planes of about equal thickness, the one on the central side staining darkly and uniformly, while the other is not stained and consequently shows distinctly. No traces of a reticulum or of chromatin granules can be seen in the first plane; but the uniform stain which this region takes indicates that the chromatin has here been dissolved in the karyolymph; therefore, I call this the solution plane.

It appears to consist of a homogeneous fluid, no structure of any kind being visible; but it is probable that a linin network still exists there, masked by the stain.

I have given the name reconstruction plane to the clear distal plane. It follows the solution plane abruptly, without any noticeable transition region between the stained and clear zones. In many cases no structure whatever is visible with a magnification of 1,600 diameters in the central side of the reconstruction plane. On the distal side, fine fibrils of chromatin appear which are connected with the reticulum of the distal part of the nucleus. These increase in thickness and number very abruptly, making thus a quite definite distal limit to the plane. It is evident that, while reconstruction of the chromatin commences in the region I have termed the reconstruction plane, it is not limited to this, but proceeds most actively in the region just distal to it, where the chromatin fibers are so suddenly thickened. The anterior portion of the plane is in fact the region where solution has been completed and chromatin (in a stainable form) has entirely disappeared, while in the posterior part of the zone chromatin is appearing.

Although I have failed many times to see any structures in the central side of the reconstruction planes, on other occasions I have observed a reticulum of extremely fine, delicately staining fibrils occupying all parts of the plane. These seem to be true linin fibrils, for it is at their nodes that the granules of chromatin first appear, and the chromatin reticulum appears to be built upon them. I believe that the linin network, even though often invisible, is always present in all parts of the reconstruction band.

The staining power of the reconstructed chromatin is considerably greater than that of the portion not yet altered. In judging the depth of stain, care must be taken to allow for the concentration of the nucleus which follows soon after the reconstruction bands pass. However, it is true that in nuclei in which concentration seems not to have begun the new chromatin stains much more vividly than the old. It frequently forms numerous masses of quite large size at the nodes of the reticulum, although just as often the chromatin knots are not present.

The margin of the undissolved (central) reticulum is usually abrupt. It often appears as in Plate IV, figure 6, closed across the face of the solution plane. On the other hand, Plate V, figure 12, shows a nucleus in which the chromatin has evidently begun to dissolve a little distance in front of the dark solution plane.

The planes of solution and reconstruction are of nearly equal thickness, their combined thickness being about the same as the width of the nucleus.

The two reconstruction bands pass toward the center of the meganucleus at equal rates until they finally meet. (Plate V, figure 14; Plate VI, figures 18, 20.) The two solution planes then unite, and presently

disappear in the usual manner, leaving the reconstruction planes joined; the new chromatin reticula advance toward the center from both sides, unite, and leave no trace of the plane of junction.

A division of the chromatin substance by one, two, or three planes is not an uncommon character of the meganuclei of the Infusoria. Bütschli mentions the presence of "Kernspalten" in Euplotes, Aspidisca, Dysteria, Nassula, Strombidium, Spirochona, and Stylonychia, and in the families Chlamydodonta, Holophryina, Trachelina, and Tintinnoina. The reconstruction bands of Euplotes were long ago observed by Stein (1859), but they do not seem to have received any attention from other authors.

The clefts (Kernspalten) in the meganuclei of Stylonychia have been the classical examples of this kind of structure, all other similar appearances apparently having been interpreted as being the same. from the account given by Bütschli, the Kernspalten of Stylonychia are structures entirely different from the reconstruction bands of Euplotes. They appear in the nuclei of Stylonychia shortly after division, disappearing as the next division begins, and usually lie a little in front of the middle of the anterior nucleus and behind the middle of the posterior one. If we agree that the two meganuclei of Stylonychia, represent not separate bodies, but a stage of precocious division of a single meganucleus, the position of the "Kernspalten" reminds us of the appearance of the reconstruction bands of Euplotes first at the opposite ends of the nucleus. Beyond this, there is no apparent resemblance either in structure or history. I do not know of any work on the "Kernspalten" of other infusoria sufficiently detailed to permit a comparison to be drawn with the reconstruction bands of Euplotes.

Balbiani, in 1895, suggested that the unstained substance in the "Kernspalten" of Stylonychia may be composed of a mass of achromatic material, or archoplasm. No substantiation of this suggestion has yet appeared, nor do the observations of nuclear division in Stylonychia indicate that the "Kernspalten" exercise any directive influence upon the process.

Whether the reconstruction bands of Euplotes are of the same nature as the "Kernspalten" of Stylonychia or not, it is certain that they are not composed of archoplasmic substance, but are regions where a solution, change, and reconstruction of the chromatin occurs. The elimination of superfluous chromatin from the nucleus has been observed to occur in numerous Protozoa, and in some Metazoa. Many different means exist for the accomplishment of this object. In some cases granules of chromatin pass bodily through the nuclear membrane into the cytoplasm, where they may remain indefinitely and perform some useful function or may be rapidly altered into unrecognizable substances. In others, the useless chromatin is extruded from the chromosomes, but dissolved within the nucleus. Elimination regularly occurs before either division or conjugation, evidently as a part of the preparation for these processes.

Metcalf describes the formation of chromatin spherules from the chromosomes of Opalina in the course of each mitosis during the year, and suggests "that these chromatin spherules are nutritive—comparable to the granules of the macronucleus of higher ciliata. Their formation and extrusion (in Opalina) is positively useful, being probably connected with nutrition and perhaps with the formation of the refractive spherules of the endosarc."

The cases of chromatin elimination heretofore described do not compare closely with the process occurring in Euplotes, since in this form there is a complete solution of all the chromatin, and not of a part only. The rapid and complete disappearance of affinity for stains from the region affected indicates that the chemical nature of the chromatin is entirely changed. The possibility exists that a vegetative chromatin is removed by osmosis during the stage of solution and that then the most active chromatin reassumes its original condition. However, it seems much more probable that an interchange of materials between nucleus and cytoplasm takes place which is of such a nature that the reconstructed chromatin is essentially a new substance, not only relieved of the so-called vegetative chromatin, but rejuvenated throughout by a physical and chemical reconstitution. The more active condition of the chromatin after the completion of this process is shown by its increased staining power.

It would seem that during the ordinary life and activities of the cell, the chromatin either accumulates a certain amount of inert substance which can play no part in the activities of division, and which it would be useless, perhaps harmful, to carry over to the daughter cells; or else that a portion of the chromatin itself is so modified by its activities that it loses some of the properties essential to its sharing in division, and therefore is eliminated before or during that process. The latter view, which is merely an expression of the fact that destructive metabolism must occur in chromatin as in all other living substance appears most reasonable. It also seems quite probable that these products of chromatin metabolism may be so closely allied to the living substance of the cytoplasm as to be incorporated with it or, if considerably degenerated, to serve as food for the cell.

The reconstruction of chromatin by complete solution and reformation, such as occurs in Euplotes, is a process of a higher order, as regards its effect on the nucleus, than that of the elimination of chromatin spherules, as in Opalina. In the latter case, much of the chromatin remaining may have been in the nucleus for a considerable time and may be practically senescent; in the former case the possibility exists that the new chromatin may be entirely composed of new material derived from the cytoplasm. As the cytoplasm itself is a constantly changing substance owing to its various katabolic and anabolic activities, an interesting possibility that the new chromatin may be formed from materials only recently entering the body is instantly suggested.

There is a large field for research in the comparative morphology and physiology of the meganuclei of the Infusoria, and for a long time to come general conclusions can not safely be drawn regarding them, their activities, and relationships. However, these observations on the meganucleus of Euplotes indicate that the meganucleus is more of an active and less of a passive agent in the cell life than many zoölogists seem to believe. The very fact that the chromatin of the meganucleus is reconstructed in a manner which must include an elimination of passive (vegetative) chromatin, such as occurs in nuclei of the ordinary type, indicates that the meganucleus is not only an aggregation of such spherules of vegetative or nutritive chromatin, but includes in addition most other properties of the ordinary cell-nucleus.

The form of the nucleus is not altered during the first half of the period of chromatin reconstruction, but as the reconstruction bands approach the center of the nucleus the phase of concentration so universal in meganuclei of this shape is entered upon. Both ends become shorter and thicker, at the same time losing any small irregularities of contour. The more nearly the reconstruction bands approach each other, the more marked becomes the shortening of the limbs of the nucleus. The central portion, that is, the part lying between the reconstruction bands, is not usually affected. Figures 14 (Plate V) and 18 (Plate VI) show that this region has increased in thickness, which is not the case in figures 8, 10, and 13 (Plate V). As the ends of the nucleus become shorter and thicker, the threads of chromatin are also changed in the same manner, so that the chromatin becomes condensed. Chromatin condensation always follows, never precedes, the reconstruction phase. fore, the center of a nucleus in which the reconstruction planes are close to each other often presents a marked contrast to the greatly concentrated ends. Unless the stain is carefully extracted the condensed portions of a nucleus appear uniformly stained, as if the chromatin network had been welded into a homogeneous mass. It is certain that the reticulum does not disappear at any stage, even that of greatest concentration, but in the last stages it is often impossible to distinguish the threads. Figure 22 (Plate VI) shows the appearance of a poorly extracted nucleus in the concentration phase, in which a reticulum is visible in only two places. After the reconstruction of the chromatin is complete, the concentration proceeds very rapidly, until the nucleus becomes a short, thick rod, varying somewhat in form, which lies in the region formerly occupied by the center of the horseshoe-shaped nucleus. The process of concentration is evidently one of contraction of both ends of the nucleus toward the center, for the latter portion of the nucleus does not move from its place.

"Bei dieser Concentrirung gegliederter Kerne muss die Membran wohl eine wesentliche Rolle spielen, da wir wissen, dass die Verbindungsfädehen häufig nur von ihr gebildet zu sein scheinen." (Bütschli, Protozoa, p. 1524.)

I do not feel that at the present time anything of value regarding the origin and purpose of the process of concentration can be added by me to the explanation Bütschli has already advanced. (Lot. cit., p. 1524.)

"Eine Erklärung für die Concentrirung des Makronucleus zu geben, scheint einstweilen kaum möglich. Active Contractionserscheinungen im gewöhnlichen Sinne dürften dabei schwerlich mitwirken. Man könnte eventuell an eine sehr einfache Deutung denken, welche jedoch etwas gewagt erscheint. Jedenfalls müssen im ruhenden Zustand besondere Einflüsse auf den band- bis rosenkranzförmigen Nucleus wirken, welche ihm die eigenthümliche Gestalt verleihen. Das einfachste, was man sich in dieser Hinsicht denken könnte, wären aussere Zugkräfte, welche ihn dehnten und zunächst bandförmig und schliesslich rosenkranzförmig werden liessen; nach Analogie mit einem zähen Flüssigkeitsfaden. welcher sich bei genügender Streckung ebenfalls perlschnurförmig gliedert. Solche Einwirkungen auf den Makronucleus könnten nur vom umgebenden Plasma ausgehen, und die Frage wäre, ob sich hierfür Anzeichen finden liessen, etwa analog den bei Isotricha beobachteten Karyophoren. Wenn nun diese Einflüsse bei Beginn der Theilung aufhörten, so würde der Nucleus von selbst wieder zu seiner natürlichen Gestalt, d. h. der kugligen bis nahezu kugligen zurückkehren.-Etwas gegründeter sind unsere Vorstellungen von der Bedeutung des Vorgangs. Wir erblicken darin, im Anschlusse an die Rouw'schen Ideen, eine Erscheinung, welche eine möglichst gleichmässige Halbirung des Nucleus inhalts, der in den langen Kernen ziemlich ungleichmässig vertheilt sein kann, bei der Theilung ermöglicht."

The period of greatest condensation is reached at a time when the body is ready to commence the process of transverse fission. The nucleus does not remain in this condition for more than a few minutes. It then elongates rapidly, forming a thick, somewhat bent rod, extending through nearly the entire length of the body. As the nucleus elongates, its reticulum of chromatin becomes more easily visible, although the condensation is still great enough to make the nucleus appear dark and solid. Possibly the chromatin may also be stained more intensely at this stage than later. As the nucleus elongates, both the anterior and posterior ends curve toward the left. (Plate VII, figure 26.) These curves increase as the constriction of the body deepens, while the middle portion of the nucleus connecting them remains straight and occupies the isthmus connecting the separating halves of the body. (Plate VII, figure 27.) As fission proceeds to the stage when the daughter animals remain connected only by a narrow neck of protoplasm (Plate VII, figure 28), the upper and lower halves of the meganucleus increase in length and also in curvature, while the straight middle portion becomes reduced to an extremely tenuous thread, which presently breaks (Plate VII, figure 29). While the nucleus is elongating, bending, and dividing, the reticulum becomes more and more plain. This is partly because the chromatin fibers become thinner and partly because of their lessened affinity for stains, rendering extraction of the stain more perfect. A noticeable feature of the reticulum at this time is the great longitudinal elongation of its meshes. This appearance of the network and the manner in which 322 GRIFFIN.

the meganucleus is pulled out into a thread at the point of division appear to be expressions of the internal tensions existing during this period, and, to a certain extent at least, are evidence supporting the theory of Bütschli quoted above, that the elongated shape of the nucleus is the result of and is maintained by cell-tensions. The contractility of the nuclear membrane and of the intranuclear reticulum are factors which seem sufficient to account for the concentration of the meganucleus, but they can not cause its elongation. During the process of concentration the karyolymph has been almost completely expelled from the nucleus. Absorption of karvolymph during expansion increases the volume of the meganucleus, but can not of itself direct expansion in particular directions. This must be accomplished by tractive force exerted upon the nucleus by the cytoplasm, of which we have visible evidence in the temporary stretching of the reticular mesh. Figures 30 and 31, Plate VII, are drawings of Euplotes immediately after fission. In figure 31, the anterior end of the nucleus still remains drawn out into a point which ends just inside the pellicle. This point, as well as other irregularities of the anterior end of the nucleus, would have been lost very quickly, for the nucleus grows into its ordinary form soon after division.

DIVISION OF THE MICRONUCLEUS.

The micronucleus divides much more quickly than the meganucleus, commencing after the reconstruction phase of the latter has started, and being completed some time before that phase has ended. The chromatin of the resting micronucleus exists in the form of a reticulum, which is only visible after thorough extraction of the stain. (Plate IV, figures 1, 2, and 3.) Soon after reconstruction of the meganucleus has been entered upon, the micronucleus increases in size to about double its ordinary dimensions. The enlargement appears to be due to an increase in the fluid contents, for no change in the chromatin can be seen.

Rearrangement of the chromatin commences when the reconstruction bands of the meganucleus have proceeded about one-quarter of their distance. The chromatin meshes first become elongated in the direction of the anterior and posterior poles of the micronucleus; next they may be found as threads reaching from end to end of the nucleus with a slightly spiral twist. (Plate V, figure 10.) It is evident that the chromatin threads are increasing in thickness and staining power. At the same time the micronucleus swells still more. The spindle is formed by the elongation of these threads of chromatin which stretch from pole to pole. (Plate IV, figure 5.) I have not been able to distinguish purely linin fibers at any stage of the ordinary division mitosis, for all spindle fibers appear to contain chromatin. Appearances in the mitosis of conjugation lead me to believe that during ordinary mitoses the linin fibrils are completely covered by or otherwise inseparably joined to the chromatin.

It is difficult to determine the number of chromosomes accurately, in spite of their small number. The usual number appears to be six or seven, although I have counted eight on a few occasions; but at other times I have been able to distinguish only four, or five. When the spindle is first fully formed the chromosomes are thickest at their middles, tapering slightly toward the ends. As division progresses the chromatin passes away from the middle of the chromosome toward the end, until finally the central portion is reduced to an extremely fine fibril connecting the considerably enlarged ends. (Plate VI, figure 19.) This still stains with chromatin stains, so does not seem to correspond exactly to the ordinary linin fibril. After the chromatin has become massed at the poles, the spindle elongates very considerably, the fibrils still joining pole to pole.

It will be seen by a comparison of figures 8, 10, 13, and 14, Plate V, that metaphase and anaphase occur with great rapidity, since there is almost no difference in the condition of the meganuclei of figures 8, 10, and 13. Stages of the micronucleus like those shown in figures 13, Plate V, and 21, Plate VI, are also extremely rare. These are the only anaphase and telophase stages I have been able to find in an examination of many hundreds of dividing individuals. The shape of each daughter micronucleus in figure 13, Plate V, shows plainly that the final step in division is a rapid separation of the poles of the spindle, while the spindle fibers remain unbroken for a considerable time. A break finally occurs at the center of the spindle and the fibers of each half of the spindle are withdrawn into their respective nuclei. A clear space is found around the micronucleus in nearly every preparation of dividing Euplotes. I can not consider this as anything but an artifact, caused by slight shrinkage of the distended and fluid-filled micronucleus.

The daughter micronuclei separate rapidly after division, quickly coming to rest at the points which will be their permanent positions in the daughter bodies. These positions are retained throughout the further processes of division.

The micronuclei rapidly assume the ordinary resting structure, and to all appearances are perfectly passive during the succeeding, most active phases of division. The short-lived activity of the micronucleus and its succeeding passivity are in marked contrast to the activities of the meganucleus and of the body as a whole. The meganucleus, supposedly a vegetative organ, exhibits far more constructive and directive activity than the micronucleus, which is usually considered to be the principal directive agent in division. The formation of chromosomes and their division in the micronucleus is a simple matter compared with the complex physical and chemical changes occurring in the chromatin of the meganucleus. The activities of the meganucleus begin with or before the first intimation of other division processes, and continue until after

fission is complete, and ordinary, normal growth is entered upon. In contrast to this the micronucleus is active during only a very short period of the division. Therefore, if a conclusion were to be drawn from the behavior of the nuclei of Euplotes, it would be that the meganucleus is not only the controlling organ in the metabolic activities of the ordinary life of the animal, but it is also the active and directive agent of ordinary (or vegetative) division, so far as any one portion of the cell can be considered independently of the others; while the micronucleus is more passive than directive, its part in division being limited to dividing in such a way as to supply each daughter cell with a micronucleus. This division appears to be more of an incidental feature of fission than one of the causative forces.

DEVELOPMENT OF THE NEW PERISTOME.

The rudiment of the new peristome appears simultaneously with or shortly after the beginning of the reconstruction of the meganucleus (Plate VI, figures 1 and 3), and in the form of a small, somewhat elongated depression just back of the posterior margin of the old peristome. The medial wall of the depression is nearly vertical, while the lateral wall curves gently and evenly. The rudiments of a row of membranellæ can be seen on the lateral wall in the earliest stages. first stages of peristome formation in E. worcesteri are quite different from the corresponding ones of E. harpa as described by Wallengren. that form a triangular area of the ectosare back of the old peristome becomes clearer than the surrounding regions, and is definitely limited between the posterior margin of the old peristome, the left-hand ventral ridge, and a new temporary elevation. The invagination of the rudiment of the new peristome occurs at the anterior end of this field, very close to the border of the old peristome. Neither the clear ectosarcal field, nor the external delimiting ridge appear in Euplotes worcesteri, nor does the rudiment of the new peristome lie so close to the border of the old peristome in that species as in E. harpa. The extremely difficult matter of finding early stages of the peristome formation in E. worcesteri would have been rendered far easier if such a change in the ectosarc had taken place.

I have also found that the rudiments of the adoral membranellæ appear considerably sooner in E. worcesteri than in E. harpa. The further development of the new peristome to its full extent is nearly the same in both species. The depression deepens and extends posteriorly, not upon the surface but beneath the ectosarc, forming a short narrow invagination. The mouth of the original depression becomes the opening of the invagination, retaining for a time about the same size and shape as first. The invagination now rapidly extends anteriorly until it nearly reaches the micronucleus. I have seen the invagination pass-

ing the micronucleus in only a few instances. The invagination extends a little farther forward in E. worcesteri than in E. harpa. At the same time it pushes a little backward and mediad and also increases considerably in width and depth. Before the invagination has attained its full length the opening to the exterior usually becomes elongated, its edges approach and finally fuse, and the new peristome exists for a time as a completely closed cavity inside the body of the Euplotes. The ventral wall of the new peristome now lies 4 or 5 μ dorsad to the old peristome.

The position of the new peristome is shown very clearly by sections. Figure 7, Plate IV, is a drawing of a transverse section of an animal in about the same stage as figure 4. The section passes just in front of the tip of the pharynx. The new peristome (P) lies below the old adoral membranellæ; inside of it the membranellæ of the new adoral zone are already well developed; as Wallengren also has observed, they move actively inside the new peristome almost from the first. Figure 16 (Plate V) was drawn from a longitudinal vertical section of a stage similar to figure 10. It passes through the old adoral zone (az) parallel to the axis of the body. Below this lies the new peristome which reaches the surface at O, where the lips of the external opening are still in contact. The membranellæ of the new adoral zone (AZ) lie outside of part of the section; at the posterior end of the cavity the membranellæ which there lie upon the outer wall are shown in transverse section. The individual cilia of the adoral membranellæ are particularly noticeable in a section like this. After remaining closed for a time the external aperture of the new peristome reopens and rapidly increases in size. (Plate V, figures 10, 13, 14; Plate VI, figures 18, 20, 22, 25; Plate VIII, figures 33, 34, 35.)

The figures show that the time at which the final opening occurs varies somewhat, using the condition of the meganucleus as a standard for comparison, and so does the rate at which the enlargement of the aperture increases. Wallengren did not observe any closure of the peristomial aperture in *Euplotes harpa*.

After the new peristome has become permanently opened, the posterior end of the cavity increases considerably in length and also bends toward the center of the body. The portion of the posterior end of the invagination which will become the pharynx is shown by Plate V, figure 10, where the rudiment of the suboral group of membranellæ (S O) lies in a slight expansion of the cavity. Since the suboral membranellæ of the adult Euplotes lie just within the mouth, it is clear that the invagination includes the rudiment of the pharynx as well as that of the peristome, and that the pharynx is formed some distance from its final position. The same peculiar bulging of the medial wall of the invagination is shown in Plate V, figure 13, although the suboral membranellæ were not visible in this specimen.

As figures 10 and 13, Plate V, were among the last drawings made, it is almost certain that the slight enlargement of the pharynx was present in other specimens (Plate V, figure 14; Plate VI, figures 18, 20, 22, 25; Plate VIII, figure 33) but not noticed at the time the sketches were made,

as its importance then was not appreciated. Plate V, figure 17, and Plate VI, figure 24, are both drawings of sections passing through the aperture of the peristomial invagination.

The further development of the peristome and pharynx proceeds as the The body of the Euplotes elongates a little before any body divides. This change in shape is made evident by the new constriction appears. peristome moving backward, as if it were pulled out from beneath the old (Plate VIII, figures 33 and 34.) By the time that the constriction of the body can be noticed, the opening of the new peristome to the exterior has become large, extending from the posterior margin of the old peristome to the posterior end of the new one. (Plate VIII, figure 34.) At the same time the anterior end of the peristomial invagination bends toward the middle of the body. Plate VIII, figures 34, 35, and 36 are successive drawings of one individual, made at intervals of about half an hour; they illustrate the manner in which constriction of the body, further increase in the size of the opening of the new peristome, and · bending of the anterior end of the new peristome toward the right, pro-In Euplotes harpa the curvature of the anterior end ceed simultaneously. of the new peristome toward the right commences at a very early stage. even before the invagination has attained its full length, and long before constriction of the body begins. There is also in that species an inward bending near the middle of the new peristome which is altogether lacking in E. worcesteri. The anterior end of the adoral zone lies in a cavity derived from the original invagination (Plate VII, figure 27, and Plate VIII, figure 36) until fission is nearly complete. As the constriction of the body deepens, the adoral zone is more and more uncovered, reaching the adult condition while the two bodies are still connected. (Plate VII, figures 28 and 29.)

While the anterior end of the peristome is passing across the end of the body, the pharynx moves still more toward the center of the body and its tip bends forward. (Plates VII and VIII, figures 26, 28, 31, 35, 36.) The widening in which the suboral membranellæ appear develops into the anterior expansion of the pharynx, in which the rows of endoral cilia appear before the constriction of the body is far advanced. (Plate VII, figure 26.)

The medial margin of the peristome is not derived from the inner edge of the growing aperture of the invagination, but from a ridge which grows forward from the anterior angle of the mouth across the medial wall of the peristomial depression. Plate VII, figure 26, Plate VIII, figures 34, 35, and 36, show successive stages in the development of this feature. As in *Euplotes harpa*, this ridge divides the right wall of the peristomial cavity into two portions; the dorsal portion becomes the inner wall of the completed peristome, while the ventral moiety becomes included in the ventral surface of the body. The part of the ventral covering of

the peristomial cavity extending out from this moiety becomes reabsorbed and leaves no ridge to mark its original relations, as in *E. harpa*. At the stage shown in figure 36, the inner margin of the peristome which has been formed in the manner just described, has united with the inner wall of the anterior portion of the peristomial invagination which still remains. By the deepening constriction of the body the outer wall of this cavity is carried away, and the medial wall becomes the margin of this side of the completed peristome. The relation of the inner edge of the aperture of the invagination to the medial margin of the completed peristome can clearly be seen by examining the cirrus marked *f* in figures 33 to 36, Plate VIII. It lies inside the original aperture, but outside of, i. e., mediad to, the true margin of the peristome.

I have carefully considered if the new peristome results from an outgrowth of the old one, and if the invagination could be formed from a linear depression of the edge of the old adoral zone, or of the region immediately lateral to that zone. There is no evidence that either of these processes occur. Instead, I have been able to follow the process of invagination, as above described, many times in living animals, and also in mounted and sectioned material. The sections leave no trace of doubt regarding the internal position of the new peristome. In the transparent living animals the adoral membranellæ of the peristomial invagination lie at a slight angle to those of the old adoral zone, and since they are all in rapid motion, the relative positions of the two zones can be determined indubitably.

The formation of the new peristome and pharynx by invagination may be a process developed in order that these parts shall be fully formed when fission commences, and to insure that the posterior daughter animal may be able to take up independent normal existence after fission without any delay. It will be noticed that all new structures, of whatever kind, are functionally complete in this animal by the time that fission is accomplished. The peristome extends so far toward the posterior end of an adult animal that a complete peristome can not be formed upon the surface of the body back of this point, while there is also little room between the left edge of the body and the margin of the peristome for such development. It should be noted that fission in this form is not merely a pinching in two of the body, but a process by which material is withdrawn from the anterior half of the body, which results in the formation of two daughter bodies very different in form from a half of the mother body at the time fission began. Therefore, the invagination of the peristome seems to be an anticipatory process related to the development of the new body and cirri.

There can be no question of overgrowth in the formation of this invagination, as in the more familiar examples of invagination among metazoan embryos. The direction of growth here is evidently controlled by internal tensions either of ectosarc or endosarc.

A process of this kind also suggests that a certain functional independence of ectosarc and endosarc exists in spite of close structural relations. The very definite and regular structure of the ectosarc has been spoken of in the first part of this paper; the process of invagination (in which the ectosarc chiefly is concerned) suggests that the relations of the primary germ layers of Metazoa may be quite definitely foreshadowed in some of the higher Protozoa.

Development of the new cirri (Plates VI, VII, and VIII, figures 25, 32, 33, 34, 35, and 36).—While the changes described in the foregoing pages have been proceeding, a new complement of cirri is developed for each half of the mother body, and all of the original cirri are absorbed. The order in which these events occur is decidedly definite. In order to follow the course of the new cirri we must distinguish each of the cirri of the fully formed body. The frontal cirri I have numbered in figure 32, Plate VII, from 1 to 7; the ones usually called abdominal cirri are numbered 8, 9 and 10; the anal cirri are I to V; the left marginal cirri are L1 and L2, while the right marginal cirri are R1, R2, and R3.

At about the time that the meganucleus reaches the condition of greatest condensation, ten slit-like, longitudinal depressions appear in two rows of five each upon the ventral surface of the body. The two complete rows appear simultaneously, and not successively, as Wallengren observed in *Euplotes harpa*.

The slits of the anterior row I have distinguished by the letters A, B, C, D, and E; those of the posterior row by a, b, c, d, and e. By combining these letters with the numbers of individual cirri, each cirrus, its origin, and its course can be indicated.

The slits are produced both by the solution of the pellicle and by depressions of the ectosarc at those points. The places where the slits appear are very definite and subject to little variation, being always practically the same as shown in Plate VII, figure 32. In this specimen cirrus 7 occupied a position a little back of its usual one. It generally stands to the right of the anterior end of slit A. (See Plate VI, figure 25.) It will be noticed that cirrus 9 stands between the posterior ends of slits C and D, and also that slit E is widely separated from D, and unlike the others of this row, points toward the edge instead of the center of the body. It also is important to observe that slits a to e arise outside of the depressions of the adult anal cirri.

There is almost no difference between Euplotes worcesteri and E. harpa in the points at which these slits appear. The only considerable difference in the origin of any of the cirri is in the case of the cirrus named F by me, and I-1 by Wallengren. This cirrus arises much farther forward in E. harpa than in E. worcesteri; the arrangement in E. harpa is such that there is much less difference in the origin of I-1 of the two daughter bodies than in E. worcesteri between cirri F and f.

The bottom of each slit becomes elevated in the form of a thin irregular ridge which is the rudiment of the cirri which presently appear in the depression. The ridge does not have the character of an undulating membrane (as described by Stein and Sterki for Stylonychia), but the shape of the depression apparently controls the form of the elevation of protoplasm from its floor. The edge presents points which seem to be the first indications of the cirri to be formed in a few moments, since in the few instances which I have been able to observe the number of points on the ridge coincided with the number of cirri to arise from that particular depression. Wallengren finds that each cirrus of E. harpa arises independently of the others in the same slit, and that there is no indication of an undulating membrane, or a protoplasmic ridge such as I describe, preceding the appearance of the cirri. He also observes the posterior cirrus of each group to appear first, followed in succession by the more anterior ones. So far as I have been able to observe, all the cirri of a group arise at the same time in E. worcesteri, although it is true that the posterior one of each group outstrips its fellows in growth from the very first.

The early development of the cirri must proceed very rapidly, for the stage in which the depressions only exist is very rarely seen among large numbers of dividing individuals. Specimens like figures 25 or 33, Plates VI and VIII, are common enough.

Three cirri arise in each depression, except in the one at the left of each row where but two appear. From the fourteen cirri thus appearing in each row are formed all the frontal, abdominal, and anal cirri of each daughter body, except one. The history of this last cirrus is peculiar, and is different in the two bodies. That of the anterior body (F) appears to the left of slit Λ , just behind cirrus 7, usually as is shown by figure 25, Plate VI. The corresponding cirrus of the posterior body (f) springs from the medial wall of the peristomial invagination, just within the aperture and immediately after its permanent opening. Neither of these cirri arises from a depression like the others.

The left marginal cirri of the two bodies also arise from depressions to the right of the old and new peristomes. (L M, l m, figures 32, 25, and 33.) The development of the left marginal cirri resembles that of the ventral cirri.

As the cirri of groups A, B, C, D, E, a, b, c, d, and e grow, the depressions in which they arise also increase, particularly in length. (Plate VI, figure 25, and Plate VIII, figure 33.) The enlargement of the grooves a, b, c, and d causes the effacement of the anterior portions of the original grooves of the anal cirri I to IV, while the portions left, in which the anal cirri still stand, are directly behind the new grooves, separated from them only by narrow oblique ridges. (Plate VIII, figure 33.) The remnants of the old grooves are effaced very soon after this stage.

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In the elongation of the groups of new cirri, the posterior one of each group remains at the point where it appeared while the anterior ones are shifted forward. In the case of the triple groups, the two anterior cirri remain close together and one behind the other until the rearrangement is nearly completed. As the new cirri approach the anterior limits of each daughter body, the anterior portions of the depressions become separated from the posterior, or open upon one side (Plate VIII, figures 34 and 35), and then gradually are obliterated. A curious feature of this process is that the left margin of the depression seems always to be the first to disappear. The portions of the grooves remaining about the posterior cirri now assume the form and position characteristic of The anterior cirrus of group (Plate I, figure 1.) the adult Euplotes. E is the first to become independent of its mate. The two of group D next lose their alignment, and separate. Those of group C follow, while the anterior pairs of B and A retain nearly the original relations until the development of the daughter bodies lacks little of being complete.

While the new cirri are developing the old ones are being absorbed, one by one. The absorption begins as soon as the new cirri appear. The first to go seems to be anal I (Plate VIII, figure 33), although 8 and 9 may disappear at the same time. Anal II follows next (Plate VI, figure 25), and then anal, V (Plate VIII, figures 34 and 36); 8 and 9 are sure to be gone by this time, and usually several of the frontal cirri, as is shown by figure 34, Plate VIII, where 4, 5, 6, and 7 have disappeared. At the time this specimen had reached the stage shown by figure 36, cirri 1 and 10 and one of the right marginals had also gone. After this it is only a matter of minutes before the remainder of the old cirri, frontals, anals, and marginals, disappear, so that by the time division is completed not one of the old cirri of the mother body remains.

The final disposition of the new cirri can be followed better from Plate VIII, figures 33 and 36, than from any description. The most peculiar thing in the course of this development is the manner in which the new frontal cirrus 4 of each body develops. This is quite different in the two bodies, yet essentially similar. The single cirrus F which develops just back of frontal 7 has been mentioned. This increases in size at the same rate as the outer new cirri, and without much change of position becomes the new frontal 4 of the anterior daughter body.

The corresponding cirrus in the posterior daughter body springs from the inner side of the peristomial aperture as soon as this reopens. (Plate VI, figures 23 and 25.) It is extremely active in its movements from the first, waving with a spiral motion so rapid and continued as to suggest that it is actively engaged in directing food into the new peristome. That this is not the case is proven by the complete absence of food balls from the peristomial invagination. For a long time this motile organ, apparently a part of the buccal apparatus, proved very puzzling. But,

as has been mentioned, it was finally observed that after the peristomial aperture has grown to a large size a ridge arises, beginning at the anterior angle of the mouth, and passing forward lateral to the cirrus just described. (Plate VIII, figures 34 and 35.) This ridge becomes the medial wall of the completed peristome, while the original medial margin of the peristomial aperture and part of the medial wall of the cavity become included in the ventral surface of the body. (Plates VII and VIII, figures 26, 34, 35, 36.) In this manner the cirrus arising in the peristomial cavity also becomes shifted to the ventral surface, and lies not far from its final position of frontal cirrus 4. (See f and f 4.)

The development of the left marginal cirri presents no noteworthy features. These cirri have reached their final positions and proportions by the time the bodies separate. Right marginals are formed upon the margins of both daughter bodies before final separation takes place, but were not observed in any of the specimens drawn.

The final disposition of the cirri is exactly the same in *Euplotes worcesteri* as in *E. harpa*. While the figures of Minkiewicz of *E. vannus* are very incomplete, the process is evidently the same in that species.

Sensory bristles.—At an early stage in the development of the cirri, numerous additional groups of granules appear upon the ventral surface. Their positions bear an evident relation to the new cirri. As each group of granules of the adult Euplotes surrounds the base of a sensory bristle, the same relation must be true of the new granules, although the direct observation of the bristles at this stage is practically impossible. I have not been able to decide whether the old sensory bristles all disappear and are replaced by new ones, or whether new bristles appear only in those portions of the two new bodies which otherwise would be left without any by the division.

The sensory bristles of the dorsal surface and their related groups of granules do not show any changes before division. New bristles apparently are interpolated in the dorsal rows during the period of growth which succeeds fission.

It has been known for many years that the old peristome, which is retained by the anterior daughter body, is not always retained without change. Confining ourselves to the genus Euplotes the only author who has mentioned in detail these changes in the old peristome is Wallengren. He finds that the mouth of Euplotes harpa atrophies so that neither food nor water is taken in during the later stages of fission. Neither his figures nor his description throw any more light upon this point. He also observed that just before division takes place the lower lip becomes filled with a great number of round granules. He did not observe any other changes in the form or structure of the peristome, nor any reconstruction of the adoral zone. I have been unable to observe any changes whatever in the old peristome of E. worcesteri during division. The

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mouth and pharynx remain open, the pharyngeal membranellæ being ordinarily active; the edges of the peristome remain as sharp as ever, and there are no signs of destruction of the adoral membranellæ. I am convinced that the old peristome continues unchanged in the anterior daughter body.

The suggestion made by Wallengren that the reason for the complicated development of new cirri and absorption of old ones among Hypotricha lies in the fact that the mother organs are not adapted to the needs of the daughter cells either in size or position, seems to me not entirely sufficient. It is often found that the new anal cirri of the posterior daughter body before division are not to be distinguished from the remaining old ones except by position. The same holds true occasionally for the frontal cirri. Division takes place in such manner that the explanation suggested by Wallengren must be true of part of the cirri. It does not appear to account sufficiently for the replacement and absorption of the cirri which are so placed that division does not seriously affect their position or action. However, in Euplotes harpa the shape of the body and the manner in which division occurs are such as to give color to Wallengren's suggestion.

DIVISION OF THE BODY.

Constriction of the body does not appear until the new cirri are all present (except the right marginals) and have moved nearly to their final positions (Plate VIII, figure 34); until the new peristome is widely open and has been drawn backward a considerable distance by the clongation of the body (note the difference in the distance from the anterior to the posterior pharynx in figures 25 and 34, Plates VI and VIII); until after the micronucleus has divided and the two daughter micronuclei have moved apart to their final positions, and the meganucleus has passed from the stage of concentration to that of elongation (Plate VI, figure 25, and Plate VII, figure 26). The constriction deepens rapidly, and separates the bodies in from one to two hours. An animal which is preparing for division is almost always considerably broader and more ovoid in outline than a "resting" individual. (Compare figures 1, 3, 25, and others, with 28 and 29, where the bodies have attained an almost typical shape before division is completed.) Even before constriction commences the body begins to grow longer and narrower. (Plate VIII, figure 33.) This change is caused by the backward growth of the region back of the old mouth, which will become the posterior individual. The movement is not simply an elongation or even an increase in mass of the posterior part of the body, but is brought about by the withdrawal of some material from the anterior portion of the body. That this must be so is proved by the backward movement of the invagination of the new peristome, which is pulled out from over the old peristome (Plate VIII, figures 33, 34, 35, Plate VII, figure 26) and by the fact that

the anterior half of the body becomes narrower at the same time. As the new peristome moves backward its anterior end is bent to the right; the fact that the inclination toward the right is greater at first than the amount of constriction of the body, indicates that pressure exerted by the latter process is not the sole cause of the bending, but that internal directive forces (or tensions) of considerable strength exist. This is still more clearly shown by Euplotes harpa, in which the peristome is bent to a right augle before constriction begins. The further bending and extension of the peristome across the anterior end of the new body proceeds at the same rate as the constriction, and appears to be produced by it. It is impossible to say certainly whether new adoral membranella are formed as the zone extends across the front of the body or not, but it seems more probable that all the membranellæ are formed in the invaginated peristomial cavity before this movement commences, and that increase in the length of the zone is secured by intercalary growth only. for this supposition is that the number of membranellæ in the invagination (Plate VII, figure 32, Plate VIII, figure 33) is equal to the entire number generally found in the adoral zone and pharynx of an adult Euplotes.

The extension of the adoral zone toward the right forces the connection between the bodies to remain at that side. (Plate VII, figures 28, 29.) As the constriction is carried across the body, the thin ventral wall of the remaining part of the peristomial cavity (Plate VIII, figure 36) is broken through; a portion remaining may form the marginal lamella of the medial wall of the completed peristome. (Plate VII, figures 28 and 29.)

The stalk connecting the daughter bodies is sometimes drawn out into a slender thread of some length; it is not unusual to see a pair of individuals swimming rapidly about connected in this manner, the posterior one swinging from side to side as if the two were engaged in a game of crack-the-whip. By the time that separation occurs the two bodies may have their usual form, or they may be of such shapes that the observer can very easily be certain which was anterior and which posterior before division. (Plate VII, figures 30 and 31.) A new contractile vacuole appears in the anterior body before fission is complete.

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ILLUSTRATIONS.

EXPLANATION OF PLATES.

The magnifications given are those which the figures possessed before reduction. Plates IV to VIII have been reduced one-half.

so, solution plane.

re, reconstruction plane.

P, new peristome.

O, definitive opening of the invaginated new peristome.

S. O., rudiment of new suboral membranellæ.

az, old adoral zone.

AZ, new adoral zone.

ph, pharynx (old).

sm, suboral membranellæ (old).

PLATE IV.

- Figs. 1, 2, 3, and 4. Successive stages in the reconstruction of the meganucleus, and of the invagination of the new peristome. × 800. Camera lucida.
- Fig. 5. Micronuclear spindle of figure 4. × 1,600.
 - 6. Posterior extremity of meganucleus of figure 3. The chromatin reticulum on the anterior side of the solution plane ends very abruptly and evenly. On the posterior side of the reconstruction plane the chromatin fibers reappear; the chromatin is nodular in the posterior part of the nucleus. × 1,600. Camera lucida.
 - 7. Transverse section of a stage corresponding to figure 4. The invagination of the new peristome (P) is seen below the old adoral zone. The new adoral membranellæ stand inside the invagination. × 600. Camera lucida.

PLATE V.

- Fig. 8. The invagination of the new peristome is completely closed. \times 800. Camera lucida.
 - Micronucleus of figure 8. Spindle threads connecting the poles could not be seen. × 1,600.
 - The peristomial invagination is reopening at O. At S. O. appears the rudiment of the new suboral group of membranelle. X 800. Camera lucida.
 - 11 and 12. Solution and reconstruction planes. Both these nuclei show a reticulum of extremely fine fibers in the reconstruction plane. These are thickest on the side away from the solution plane; little masses of chromatin can be seen forming at the nodes. × 1,600. Camera lucida.
 - 13. The opening of the new peristome is enlarging. The micronucleus has divided, the two new micronuclei still showing the points at which the nuclear membrane was drawn out as the poles moved apart. × 800. Camera lucida.
 - 14. The new peristome now has a large opening. The two micronuclei are entirely reconstructed, and have assumed their final positions. The reconstruction bands of the meganucleus are approaching each other, while the meganucleus as a whole is condensing and shortening. × 800. Camera lucida.

- Fig. 15. The middle portion of the meganucleus of figure 14. imes 1,200. Camera lucida.
 - 16. A vertical longitudinal section of the new peristome at a stage corresponding to figure 10. The invaginated new peristome forms an extensive cavity lying directly dorsad (below in the figure) to the old adoral zone (az). The opening of the invagination to the exterior at O is just commencing. The new adoral zone is seen at AZ. × 1,000. Camera lucida.
 - 17. An obliquely transverse section of a stage corresponding to figure 14, passing through the new peristome and its opening, and the old adoral zone (az). × 600. Camera lucida.

PLATE VI.

- Fig. 18. The two solution planes of the meganucleus have met. The meganucleus is considerably condensed. × 800. Camera lucida.
 - 19. Anaphase of micronucleus.
 - 20. The solution planes have disappeared and the reconstruction planes have met. × 800. Camera lucida.
 - 21. Late anaphase of micronucleus.
 - 22. The reconstruction planes have disappeared and most of the meganucleus has condensed until the chromatin reticulum is not easily visible. × 800. Camera lucida.
 - 23. At about the same stage as figure 22, but with a less condensed meganucleus. The rudiments of the new cirri have been formed.
 - 24. A transverse section passing through the old peristome, pharynx, adoral zone and suboral membranellæ, and also through the new peristome and its opening to the exterior. The latter is at the base of a depression of the outer surface, and one of its edges is shown in the figure. × 400. Camera lucida.
 - 25. The final stage in the condensation of the meganucleus. Two of the old anal cirri have disappeared; the new cirri are increasing in size.

PLATE VII.

- Figs. 26 to 29. Elongation and constriction of the body and meganucleus; the new peristome is drawing out from above the old, and assuming its definite position.
- Fig. 30. Anterior daughter individual immediately after division.
 - 31. Posterior daughter individual immediately after division.
 - 32. First stage in the development of the new cirri. A, B, C, D, E, depressions in which the new cirri of the anterior daughter body will develop; a, b, c, d, e, corresponding depressions of the posterior daughter body; 1, 2, 3, 4, 5, 6, 7, frontal cirri; 8, 9, 10, abdominal cirri; I, II, III, IV, V, anal cirri; L1, L2, left marginal cirri; R1, R2, R3, right marginal cirri.

PLATE VIII.

Figs. 33 to 36. Successive stages in the development and arrangement of the new cirri, and in the resorption of the old ones. Figures 34, 35, and 36 are drawn from the same individual at intervals of about half an hour.

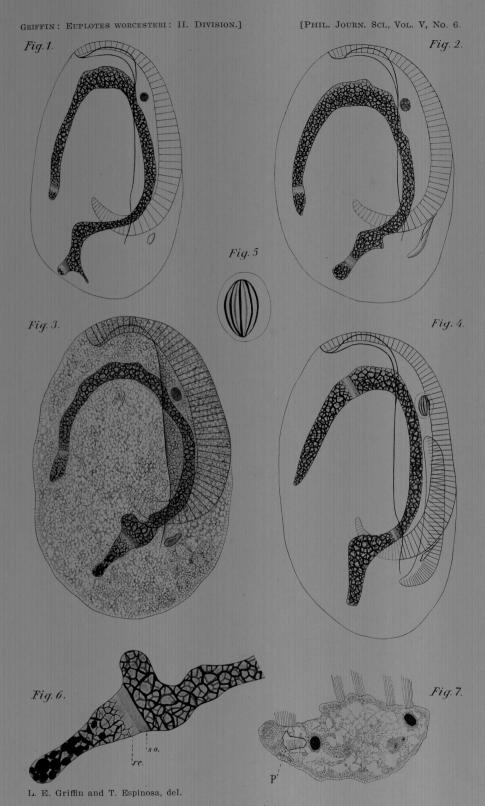


PLATE IV.

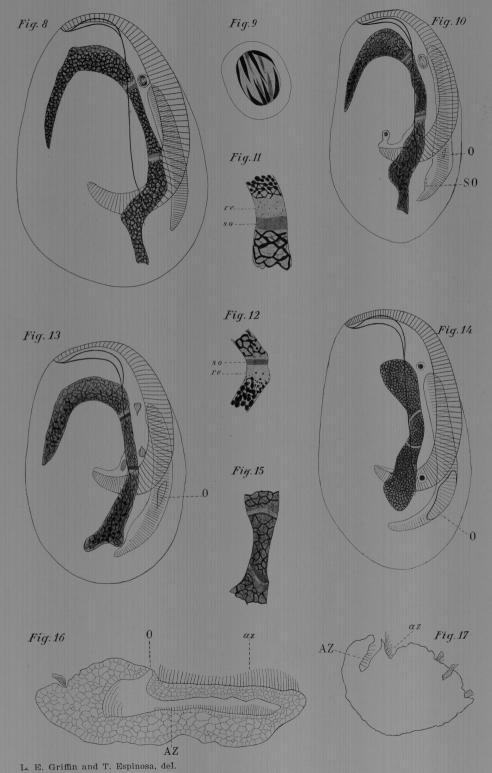


PLATE V.

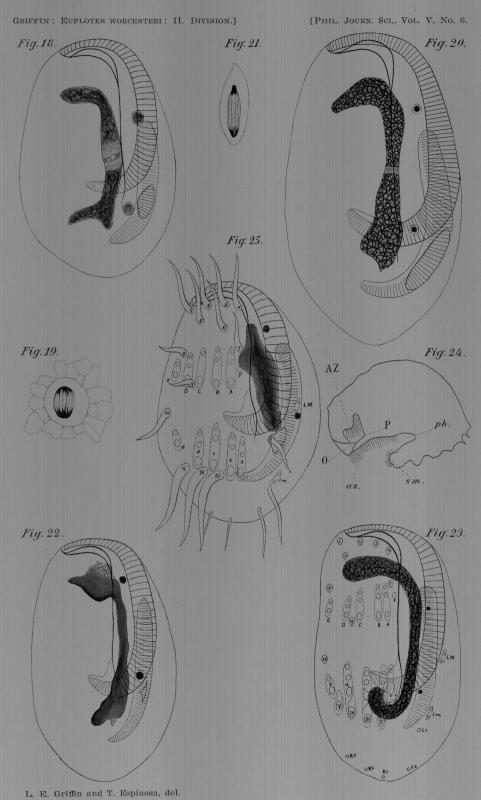


PLATE VI.

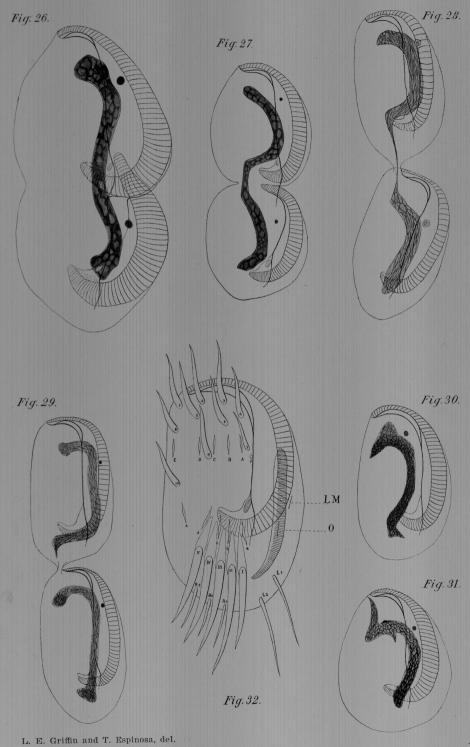
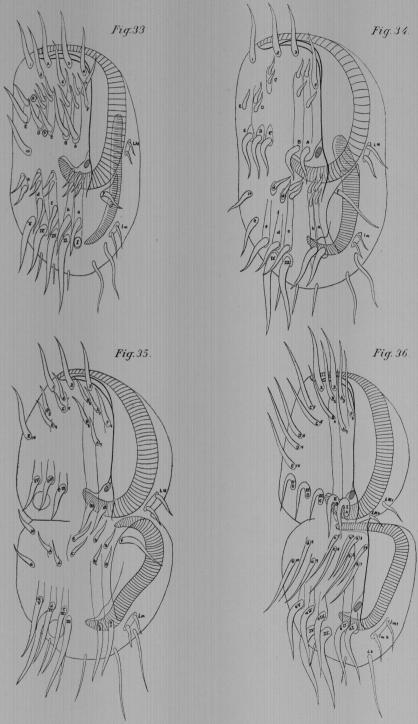


PLATE VII.



L. E. Griffin and T. Espinosa, del.

REVIEW.

Aigrettes and Birdskins. The Truth About Their Collection and Export. By Harold Hamel Smith, editor of "Tropical Life." With a foreword by Sir J. D. Rees, K. C. I. E., C. V. O., M. P. Cloth. Pp. 138. Price: 5 shillings. London: John Bales Sons & Danielson, Ltd. 1910.

This book is written in defense of the bird-millinery trade and in protest against a notification issued in India, in 1902, prohibiting the export from British India of the skins and feathers of all birds other than domestic birds, ostrich feathers and skins, and bona fide natural history specimens.

The objection to this order is that while it does not protect the birds from being killed it takes from the poorer classes in India a considerable source of income.

The author claims that the collecting of feathers of wild birds can not be considered cruel, unless it be considered cruel to shoot game for sport, and that, taking the world as a whole, birds are not in danger of extermination, or even of becoming rare.

It is stated that, "unlike the milliners who need the birds only for a few years at a time, whilst the fashion for wearing them lasts, the suppliers to natural history museums and the fishing-tackle trade go on collecting uninterruptedly year after year, as they have no fashion to interrupt their demand."

Members of the Audubon societies and other protectionists will be pleased to learn that should any fear of the extermination of a certain species arise "the trade wisely and very naturally will be only too pleased to collaborate with any official body to keep that particular species out of fashion until their numbers have increased sufficiently to warrant their being used again."

The extermination of some species of birds, such as the herons in Florida, is charged to the advance of civilization and the opening of new country. The author suggests the appointment of a permanent international committee to be consulted at any time, to inquire into reported scarcity of birds, and to ascertain on independent evidence how correct the reports are. The committee should, if necessary, proceed to the center of origin and ascertain the true state of the case.

The frontispiece is a half-tone portrait of the author.

R. C. McG.

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